

## ***Racocetra cromosomica* sp. nov. from Oaxaca, Mexico**

EDUARDO CHIMAL-SÁNCHEZ<sup>1,2</sup>, IRMA REYES-JARAMILLO<sup>1</sup>,  
SARA LUCÍA CAMARGO-RICALDE<sup>1</sup>, LUCÍA VARELA<sup>1</sup>,  
JOSE YABÍN SALMERÓN CASTRO<sup>1</sup>, NOÉ MANUEL MONTAÑO<sup>1\*</sup>

<sup>1</sup>Departamento de Biología, División de Ciencias Biológicas y de la Salud,  
Universidad Autónoma Metropolitana-Iztapalapa,  
Av. San Rafael Atlixco 186, Col. Vicentina, 09340, Ciudad de México, México

<sup>2</sup>Facultad de Estudios Superiores–Zaragoza, Universidad Nacional Autónoma de México,  
Batalla del 5 de Mayo s/n, Col. Ejército de Oriente, 09230, Ciudad de México, México

\*CORRESPONDENCE TO: [nmma@xanum.uam.mx](mailto:nmma@xanum.uam.mx)

**ABSTRACT**—Analysis of soil samples collected in the rhizosphere of *Agave karwinskii* in the Central Valleys of Oaxaca, Mexico, revealed an undescribed species of *Racocetra* that possesses ornamented spores. The ornamentation on the outer layer of the external spore wall consisted of rounded and elongated processes, which are organized in such a way that they look like chromosomes. Therefore, the new species was named *Racocetra cromosomica*. It is the first species of *Racocetraceae* (*Gigasporales*) described from Oaxaca, one of the Mexican states having the greatest floristic diversity.

**KEY WORDS**—arbuscular mycorrhizal fungi, *Glomeromycota*, mezcal, semiarid ecosystems, taxonomy

## **Introduction**

Mexico has a wide variety of ecosystems, and it is the center of origin, diversification and domestication of several plant species (Casas 2019). Oaxaca is one of the Mexican states characterized by the highest floristic diversity, comprising 8431 plant species (García-Mendoza & al. 2004). The diversity in Oaxaca arises from the convergence of five biogeographical provinces varying in climates, soils, and vegetation types (Morrone 2019), such as xerophilous scrublands and tropical dry forests, containing plants

of *Agavaceae*, a family endemic to America and one of ten monocot families with the highest species richness. In Oaxaca, the *Agave* genus is highly diverse, containing 32 of the 159 taxa distributed in Mexico (García-Mendoza & Galván 1995, García-Mendoza & al. 2004), all with great ecological, economic, and cultural importance for the inhabitants (Torres-García & al. 2019). Several *Agave* species are used to prepare mezcal, and people identify both agaves and mezcal as symbols of cultural identity. In preparing mezcal in the Central Valleys and the Sierra Sur of Oaxaca, people use *Agave vivipara* L. [= *A. angustifolia* Haw.], known in Mexico as agave espadín, and some wild species, as *Agave karwinskii* Zucc. (Ordoñez & Rodríguez 2008, García-Mendoza & al. 2004, 2017). Several *Agave* species are listed in the IUCN-Red List of Threatened species, including *A. karwinskii*, due to its limited distribution range (14,492 km<sup>2</sup>) and the rapidly increasing demand for mature individuals for mezcal production (García-Mendoza & al. 2019).

Arbuscular mycorrhizal fungi (AMF) species (*Glomeromycota*) form mutualist symbiosis with almost 85% of land plant families, including *Agavaceae* (Carballar-Hernández & al. 2013, Goto & al. 2013; Chimal-Sánchez & al. 2018), and they promote the growth and nutrition for most plants (Smith & Read 2008), including *A. tequilana* F.A.C. Weber 'Azul' (Montoya-Martínez & al. 2019). Thus, in Mexico, AMF could be very important not only for conservation of floristic diversity but also for production of agave plants. In Mexico, currently 160 species of AMF are registered; however, the morphology of many AMF species found in the country suggests that they are undescribed (Varela & al. 2019, Polo-Marcial & al. 2021).

During a study on AMF associated with rhizosphere soil of mezcal agaves (*A. vivipara*, *A. karwinskii*) in the Central Valleys and Sierra Sur of Oaxaca, Mexico (the mezcal range), four new records and 48 morphospecies were registered (Chimal-Sánchez & al. 2018, Reyes-Jaramillo & al. 2019); however, ca. 30% of the AMF listed exhibit a morphology that does not fit those described species. Among them is a member of *Racocetraceae* (for this family see: Silva & al. 2012, Goto & al. 2012, Souza & al. 2018, Wijayawardene & al. 2020) that was registered in the rhizosphere of *A. karwinskii* and reported as *Racocetra* sp. 1 by Reyes-Jaramillo & al. (2019). Its subcellular spore structure, germination shield morphology, and histochemical properties indicates that it does belong in *Racocetra* (*Gigasporales*). Most importantly, spores of this fungus have a unique ornamentation consisting of chromosome-like outgrowths. Therefore, the fungus is here described as *Racocetra cromosomica*.

## Materials & methods

The Central Valleys (CV) and Sierra Sur of Oaxaca (SSO) are two of the eight economic regions of the State of Oaxaca. The CV and SSO belong to the “Sierra Madre del Sur” biogeographic province (Morrone 2019). The climate of the region is semi-dry, warm to semi-warm, with rains in summer. The soils according to World Reference Base for Soil Resources (WRB 2014) are Regosols and Leptosols, although Calcisols and Phaeozems are also present. The vegetation corresponds to tropical dry forests and xerophytic scrubland that have been strongly altered by agricultural activities, so that there are only fragments of this vegetation, with wild populations of *A. karwinskii* and cultivated fields with *A. vivipara* (INEGI 2010, Reyes-Jaramillo & al. 2019).

In the Central Valleys and Sierra Sur of Oaxaca, seven study sites (S) with wild populations of *A. karwinskii* were established in the municipalities of San Pedro Totolapan (S1), San Agustín Amatengo (S3, S4), Ejutla (S5), and San Luis Amatlán (S6, S9), while only two sites were established in fields cultivated with *Agave vivipara* in Ejutla (S2) and San Luis Amatlán (S7). The soils have a texture of Loamy sand (S1, S3–S9) or Sandy loam (S2), and pH ranging from neutral (S1, pH = 7.5; S2, pH = 7.19, and S3, pH = 7.28) to lightly alkaline (S4, pH = 7.86; S5, pH = 8.06; S6, pH = 8.02; S7, pH = 8.04; S8, pH = 7.96, and S9, pH = 8.0). On average, they are rich in organic matter (OM = 2.65% from S1–S4; OM = 4.9% from S5–S9), poor in available phosphorus ( $\text{PO}_4$ -Olsen = 1.6 mg kg<sup>-1</sup>), and rich in extractable bases of calcium and magnesium, but low in potassium and sodium (Reyes-Jaramillo & al. 2019). However, our new *Racocetra* species was registered only in San Agustín Amatengo (S3) in soil with the highest percentage of sand (79%). Our new *Racocetra* coexisted with other AMF species, the most frequent of were *Acaulospora rehmsii* Sieverd. & S. Toro, *A. scrobiculata* Trappe, *Cetraspora pellucida* (T.H. Nicolson & N.C. Schenck) Oehl & al., *Gigaspora gigantea* (T.H. Nicolson & Gerd.) Gerd. & Trappe, *Funneliformis halonatus* (S.L. Rose & Trappe) Oehl & al., *F. mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler, and *Racocetra fulgida* (Koske & C. Walker) Oehl & al. (Reyes-Jaramillo & al. 2019).

Pot trap cultures were established with native soil samples (600g per pot) and grown without fertilization in glasshouse conditions (Stutz & Morton 1996) using corn (*Zea mays* L.) and “guaje” (*Leucaena* sp., *Leguminosae*) as host plants. Host plants were grown for six months and watered every third day with distilled water, and then left to dry for two weeks to favor formation of AMF spores. Due to the small number of *Racocetra* spores obtained (1 spore per 300 g dry soil), only one single-species culture was set using two spores as inoculum and the same host plants. Unfortunately, this attempt failed, and no newly produced spores and mycorrhizal structures were found. Consequently, the new *Racocetra* species is here described based on field-collected spores and those extracted from trap cultures.

*Racocetra* spores were isolated by wet sieving and decanting (Gerdemann & Nicolson 1963), followed by centrifugation in 60% sucrose solution to eliminate organic matter and mineral remains. Several spores were then placed in Petri

dishes with distilled water, and their color was determined under a dissection microscope using the web color chart hosted by the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM 2018). Ten spores were mounted on microscopic slides in polyvinyl alcohol lacto-glycerol (PVLG) and in PVLG mixed with Melzer's reagent 1:1 (v/v). Terminology for the species description, spore characteristics, and spore wall nomenclature are those adopted from Walker (1983) and Oehl & al. (2008). Likewise, we used an updated taxonomic key for *Racocetra* species proposed by Souza & al. (2018). Voucher specimens were deposited in the Herbarium of Instituto Politécnico Nacional, Mexico City, Mexico (ENCB), the Herbarium of Universidad Autónoma de Tlaxcala, Tlaxcala state, Mexico (TLXM), and the Laboratory of Legume Biosystematics, Department of Biology, Universidad Autónoma Metropolitana-Iztapalapa, Mexico City, Mexico (UAMI).

### Taxonomy

***Racocetra cromosomica*** Chim.-Sánchez, Varela & Montaña, **sp. nov.**

FIGS 1, 2

IF 557326

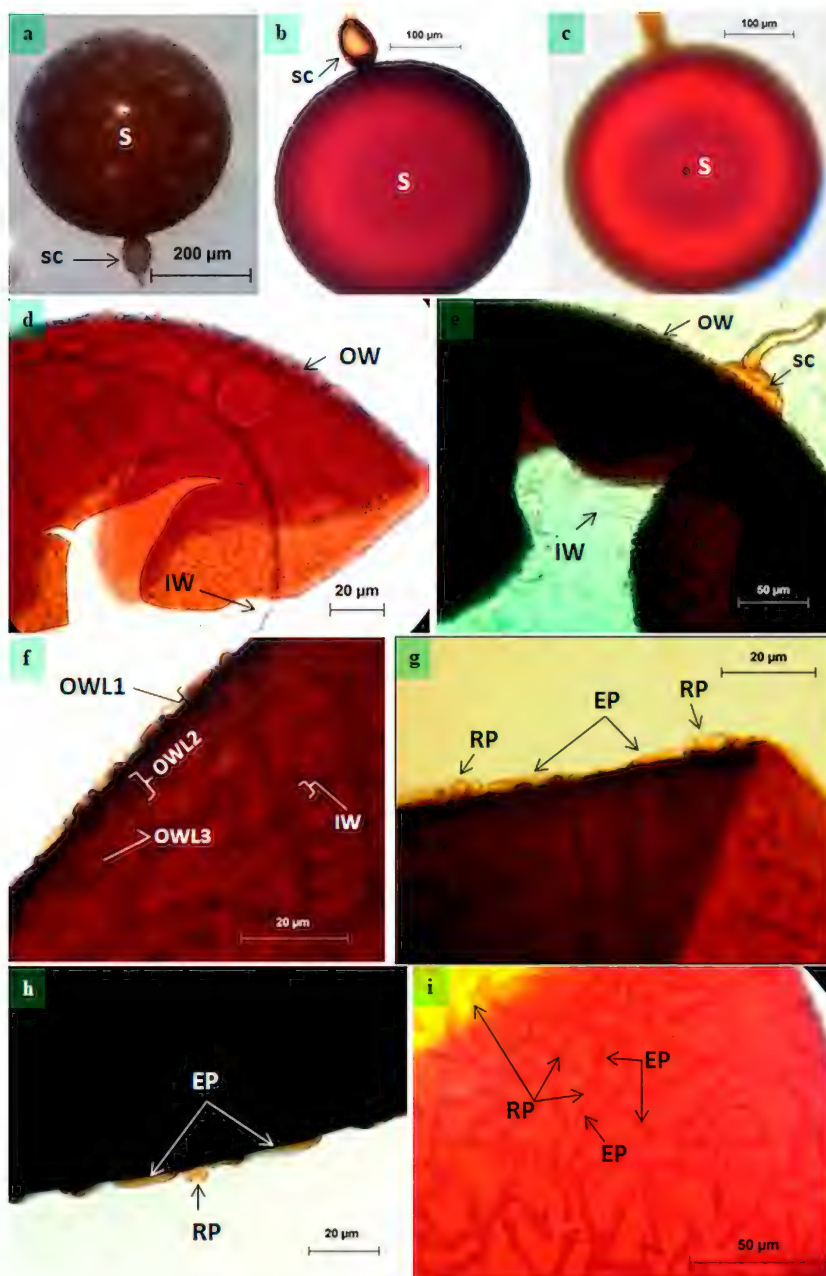
Differs from all other *Racocetra* and gigasporalean species by its unique ornamentation formed on the outer spore wall, consisting of rounded and elongated processes resembling condensed chromosomes.

TYPE—Mexico, Oaxaca, Central Valleys in San Agustín Amatengo, 16°31'06"N 96°47'08"W; isolated from the rhizospheric soil of *Agave karwinskii* growing within a xerophytic scrubland (SAASM) and coming from a propagation pot (SAASM-Prop) with *Zea mays* and *Leucaena* sp. (guaje) as trap plants; isolated June 2017, E. Chimal-Sánchez (**Holotype**, ENCB121802 [SAASM-Prop-slide-001]; **isotypes**, TLXM-5034 [SAASM-Prop-slide-002], UAMI-002 [SAASM-Prop-slide-003]).

ETYMOLOGY—referring to the distinctive ornamentation (rounded and elongated processes) on the outer spore wall that resembles chromosomes.

**SPORO-CARP** formation is unknown. Spores are formed singly in the soil and terminally on a bulbous sporogenous cell. Spores are red-brown (20–80–60–0) to dark red-brown (60–80–100–0); globose, 368.6–445.3 µm.

FIG. 1. *Racocetra cromosomica* (holotype, ENCB121802): a, b. Spore (S) in water (a) and PVLG (b) with bulbous sporogenous cell (sc) characteristic of the *Gigasporales*; c. The spore surface of an intact spore ornamented with elongated processes seen in plan view; d. Outer spore wall (OW) separated from inner spore wall (IW) of a crushed spore; the unique chromosome-like processes ornamenting the upper surface of the outer spore wall are visible; e. Outer (OW) and inner (IW) spore wall and bulbous sporogenous cell with no reaction in Melzer's reagent; f. Outer spore wall with three permanent layers (OWL1–3), of which OWL1 is ornamented, and inner spore wall (IW); g, h. The upper surface of layer 1 of the outer spore wall ornamented with rounded (RP) and elongated (EP) processes; i. The distribution and arrangement of rounded (RP) and elongated (EP) processes (chromosomes-like) on the spore surface.



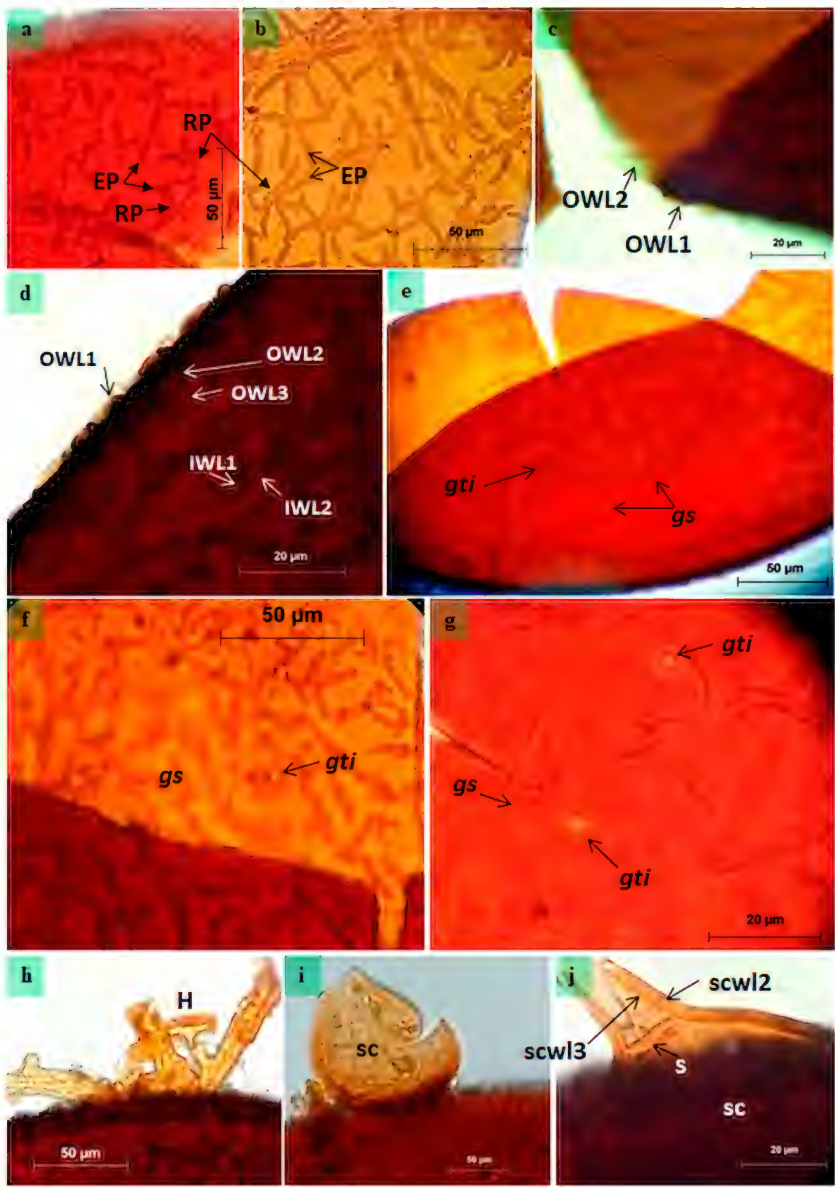
SPORE WALL comprising two walls: an outer wall (OW) and an inner wall (IW). OW has three closely adherent layers (OWL1, OWL2, and OWL3) of a total thickness of (15.4–)16.6(–17.6)  $\mu\text{m}$ . OWL1 is a permanent rigid layer, yellow-brown (0–10–40–0) to dark red-brown (60–80–100–0). The surface of this layer has double ornamentation resembling condensed chromosomes when observed in plan view. The first ornamentation type comprises rounded processes, (1.9–)3.7(–5.4)  $\mu\text{m}$  high and (3.8–)4.8(–5.7)  $\mu\text{m}$  wide at their base. Regularly, these processes are arranged in groups of 2, 4, 6, 8, or more, and when grouped they have a width of (11.1–)11.9(–12.7)  $\mu\text{m}$  and a height of (4.9–)5.1(–5.4)  $\mu\text{m}$ . The second type of ornamentation consists of elongated outgrowths, which are fused to the rounded ones and 1, 2, 3 or 4 elongated processes may be attached. In addition, the elongated processes may be connected to another group of rounded processes forming an irregular reticulum when the spores are observed in plan view. The elongated processes are claviform, (10.5–)16.4(–21.2)  $\mu\text{m}$  long, (4.4–)5.2(–6.5)  $\mu\text{m}$  wide, and (2.8–)3.4(–4.3)  $\mu\text{m}$  high. Both types of ornamentations are yellow-brown (0–10–40–0) to dark red-brown (60–80–100–0). The second layer of the spore wall (IWL2) is laminated, (9.1–)10.3(–12.4)  $\mu\text{m}$  thick, smooth, and hyaline (20–0–20–0). OWL3 is hyaline, often difficult to observe as it closely adheres to OWL2, <1  $\mu\text{m}$  thick. None of the spore wall layers stained in Melzer's reagent.

INNER WALL has two adherent layers (IWL1 and IWL2) that are semi-flexible, hyaline (30–0–20–0), jointly <5  $\mu\text{m}$  thick, and do not stain in Melzer's reagent.

GERMINATION SHIELD formed on the outer surface of IW. It is hyaline (20–0–20–0), oval, (149.7–)165.5(–181.7)  $\mu\text{m}$  long  $\times$  (102.4–)126.5(–140.9)

---

FIG. 2. *Racocetra cromosomica* (isotype, TLXM-5034): a, b. The arrangement and shapes of rounded (RP) and elongated (EP) processes (chromosomes-like) on layer 1 of the outer spore wall from spores crushed in Melzer's reagent; c. Ornamented, dark-colored layer 1 (OWL1) and smooth, colorless layer 2 (OWL2) of the outer spore wall; d. Three-layered outer spore wall (OWL1–3) and two-layered inner spore wall (IWL1–2); e–g. Spores with germination shields (gs) composed by multiple small compartments (6–8), each with generally one germ tube initiations (gti); h. Germination from gti; note the thick and reddish brown color of the hyphae (H); i, j. Subglobose to ovoid sporogenous cell (sc) with a septum (S) at its base; note sc has no ornamentations and its wall consists of only two layers (scwl2 and scwl3) continuous with outer spore wall layers 2 and 3.



$\mu\text{m}$  wide, multilobed (6-8), each lobe generally with one germ tube initial (gti) from where germination tubes emerge.

**BULBOUS SPOROGENOUS CELL** formed terminally from an extraradical mycorrhizal hypha, yellow brown (20-40-100-0), sub-globose to ovoid, (56.1-)-61.3(-63.9)  $\mu\text{m}$  wide and (68.9-)-74.6(-77)  $\mu\text{m}$  long in the region from the spore base to the subtending hypha septum. Sporogenous cell wall smooth with two layers (scwl2, scwl3) continuous with OWL2 and OWL3. Scwl1 is absent since the bulb does not have the ornate layer of the spores (OWL1), scwl2 is yellow-brown (20-40-100-0), 2-3  $\mu\text{m}$  thick, and scwl3 is yellow (0-30-80-0), 1.1-1.4  $\mu\text{m}$  thick.

**AUXILIARY CELLS** were not observed.

**DISTRIBUTION & ECOLOGY** — *Racocetra cromosomica* is known only from Central Valleys, San Agustín Amatengo, Oaxaca, Mexico. The spores of *R. cromosomica* have been recorded only from soil associated with the rhizosphere of *A. karwinskii* growing in a xerophilous scrubland with remnants of other *A. karwinskii* wild populations. Soil characteristics are loamy sandy (79% sand),  $\text{pH}_{\text{H}_2\text{O}} = 7.2$ , soil organic matter = 3.2%, available phosphorus ( $\text{PO}_4^-$ -Olsen) = 0.7  $\text{mg kg}^{-1}$ , Ca = 15  $\text{cmoles}_{(+)} \text{kg}^{-1}$ , Mg = 7.5  $\text{cmoles}_{(+)} \text{kg}^{-1}$ , K = 0.29  $\text{cmoles}_{(+)} \text{kg}^{-1}$ , and Na = 0.14  $\text{cmoles}_{(+)} \text{kg}^{-1}$  (Reyes-Jaramillo & al. 2019). *Racocetra cromosomica* probably has preference for sandy soils like other *Gigasporales* (Lekberg & al. 2007; Vieira & al. 2020).

**MYCORRHIZAL ASSOCIATIONS** unknown. In the AMF multi-species propagation pot, *R. cromosomica* was propagated with maize (*Zea mays*) and “guaje” (*Leucaena* sp.) as host plants, but its sporulation was very low (one spore per 300 g dry soil). However, the presence of spores in these cultures suggested that *R. cromosomica* formed arbuscular mycorrhiza, as do other *Racocetra* species grown in single-species cultures.

## Discussion

The formation of spores from a bulbous sporogenous cell, the subcellular structure of spores containing two spore walls, the features of the spore germination shield, and the lack of staining reaction of the inner spore wall in Melzer's reagent unambiguously support the fungus collected by us in Mexico and here described as a new species of *Racocetra*.

The ornamentation of the upper surface of *Racocetra cromosomica* spores, consisting of rounded and elongated processes that are organized as if they were chromosomes, is a unique and very important diagnostic character that easily distinguishes this species from other *Racocetra* species and species



of other gigasporalean genera producing ornamented spores. Spores of *R. undulata* T.C. Lin & C.H. Yen are much smaller (195–225  $\mu\text{m}$  vs. 368.6–445.3  $\mu\text{m}$ ) and are ornamented with pit undulations (Lin & Yen 2011), and the spore ornamentation in *R. persica* (Koske & C. Walker) Oehl & al., consists of fine spines (Oehl & al. 2008, Souza & al. 2018). *Racocetra minuta* (Ferrer & R.A. Herrera) Oehl & al., has a double ornamentation on the outer spore wall, but this ornamentation is composed of projections with central depressions (Oehl & al. 2008, Souza & al. 2018). *Intraornatospora intraornata* Goto & al., ( $\equiv$  *R. intraornata* B.T. Goto & Oehl) produces ornamented gigasporoid spores, but the ornamentation consists of densely packed tubes that, importantly, occur on the lower surface of a laminate layer of the outer spore wall (Goto & al. 2009, 2012).

The only *Racocetra* species that have spores ornamented with processes (outgrowths resembling warts) are *R. beninensis* Oehl & al., *R. verrucosa* (Koske & C. Walker) Oehl & al., *R. coralloidea* (Trappe & al.) Oehl & al., *R. gregaria* (N.C. Schenck & T.H. Nicolson) Oehl & al., and *R. crispa* F.A. Souza & al. However, the spores of both *R. beninensis* and *R. verrucosa* are lighter in color and ornamented with processes that are smaller (0.9–2.1(–2.8)  $\mu\text{m}$  long, 0.9–3.8  $\mu\text{m}$  wide in *R. beninensis*; 0.5–1.5  $\mu\text{m}$  long, 0.5–1.5  $\mu\text{m}$  wide in *R. verrucosa*) and simpler in construction (Koske & Walker 1985, Tchabi & al. 2009). *Racocetra coralloidea* spores are ornamented with flattened warts with angular margins (most 2–12  $\mu\text{m}$  wide  $\times$  1–3  $\mu\text{m}$  high) and those of *R. gregaria* with rounded warts (most 11–26.7  $\mu\text{m}$  wide  $\times$  3–7  $\mu\text{m}$  high) that differ in size and are clearly separated from each other, never occurring in groups as in *R. cromosomica* (Oehl & al. 2008, Souza & al. 2018). The ornamentation of *R. crispa* clearly differs from that of *R. cromosomica* by displaying multiple cloud-like projections with a basal diameter of (5–)15–41  $\mu\text{m}$  and a height of (5.2–)9.5–18  $\mu\text{m}$  (Souza & al. 2018).

Other species of the *Gigasporales* that can be morphologically confused with *R. cromosomica* due to the formation of similarly colored ornamented spores are *Scutellospora dipapillosa* (C. Walker & Koske) C. Walker & F.E. Sanders, *Dentiscutata colliculosa* B.T. Goto & Oehl, *D. nigerita* Khade, *D. nigra* (J.F. Redhead) Sieverd. & al., and *D. reticulata* (Koske & al.) Sieverd. & al. Apart from morphological differences in the spore ornamentation, these species also differ from *R. cromosomica* by possessing three spore walls instead of two (Koske & Walker 1985, Goto & al. 2010, Khade 2010, Oehl & al. 2008).

Although *R. cromosomica* sporulated in multi-species trap cultures, the low numbers of spores obtained did not allow us to conduct molecular and phylogenetic analyses to determine the position of this species among sequenced *Racocetra* spp. Nonetheless its spore morphology both clearly

supports its novelty and easily distinguishes *R. cromosomica* from other ornate species in the *Gigasporales*.

We are aware that *R. cromosomica* should be characterized molecularly in the future to track occurrence elsewhere based on environmental studies. Finally, the fact that *R. cromosomica* has so far been found only in the rhizosphere of *A. karwinskii*, a highly vulnerable species endemic to Mexico, suggests that *A. karwinskii* is critical for in situ conservation of this mycorrhizal fungus and that this new *Glomeromycota* species could be essential in the recovery of *A. karwinskii* populations within mezcal producing regions in Oaxaca, Mexico, particularly in the town of San Agustín Amatengo.

### Acknowledgements

We thank Genaro Sierra for his support in the field collection in the town of Ejutla, Oaxaca as well as Rosalva García Sánchez, Alejandro Alarcón, Ronald Ferrera Cerrato, Sandra Cortés; Maria Eugenia Fraile, and Rosaura Grether for their support with the microphotographs. L. Varela was supported by the professorship “Ramón Riba y Nava Esparza” at the Universidad Autónoma Metropolitana-Iztapalapa. We thank Janusz Błazkowski (West Pomeranian University of Technology, Szczecin Poland) and Bruno Tomio Goto (Universidade Federal do Rio Grande do Norte, Brazil) for reviewing our manuscript and their helpful, constructive comments and suggestions that improved this paper. We are also grateful to Nomenclature Editor Shaun Pennycook and Editor-in-Chief Lorelei L. Norvell for their excellent reviews.

### Literature cited

- Carballar-Hernández S, Palma-Cruz FJ, Hernández-Cuevas L, Robles C. 2013. Arbuscular mycorrhizal potential and mycorrhizal fungi diversity associated with *Agave potatorum* Zucc. in Oaxaca, Mexico. *Ecological Research* 28: 217–226. <https://doi.org/10.1007/s11284-012-1008-7>
- Casas A, Torres I, Parra F, Torres J. 2019. Centros de origen y diversificación de plantas cultivadas en América. In: JJ Torres-Guevara & al. (eds). *De los cultivos nativos y el cambio del clima: Hallazgos*. UNALM-Perú, UNAM-México, CCTA-Andes, Lima, Perú.
- Chimal-Sánchez E, Reyes-Jaramillo I, Salmerón-Castro JY, Vázquez-Pérez N, Varela-Fregoso L. 2018. Cuatro nuevos registros de hongos micorrizógenos arbusculares (*Glomeromycota*) asociados con *Agave karwinskii* y *A. angustifolia* (*Agavaceae*) de Oaxaca, México. *Acta Botánica Mexicana* 125: 173–187. <https://doi.org/10.21829/abm125.2018.1356>
- García-Mendoza A, Galván R. 1995. Riqueza de las familias *Agavaceae* y *Nolinaceae* en México. *Boletín de la Sociedad Botánica de México* 56: 7–24. <https://doi.org/10.17129/botsoci.1461>
- García-Mendoza AJ, Ordoñez MJ, Briones-Salas M. 2004. Biodiversidad de Oaxaca. 1ª edición. Ciudad de México, México. Universidad Nacional Autónoma de México, Fondo Oaxaqueño para la Conservación de la Naturaleza y World Wildlife Fund.
- García-Mendoza AJ, Cházaro BMJ, Nieto SJ, Sánchez TLF, Tapia CE & al. 2017. 1Agaves. 15–68, in: *Panorama del Aprovechamiento de los Agaves en México*. Guadalajara, Jalisco, México.

- García-Mendoza AJ, Torres-García I, Casas A, Sandoval-Gutiérrez D. 2019. *Agave karwinskii*, Cachitún. The IUCN Red List of Threatened Species 2019. <https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T115630856A116354018.en>
- Gerdemann JW, Nicolson TH. 1963. Spores of mycorrhizal *Endogone* species extracted from soil by wet sieving and decanting. Transactions of the British Mycological Society 46: 235–244. [https://doi.org/10.1016/S0007-1536\(63\)80079-0](https://doi.org/10.1016/S0007-1536(63)80079-0)
- Goto BT, Maia LC, Silva GA, Oehl F. 2009. *Racocetra intraornata*, a new species in the *Glomeromycetes* with a unique spore wall structure. Mycotaxon 109: 483–491. <https://doi.org/10.5248/109.483>
- Goto BT, Silva GA, Maia LC, Oehl F. 2010. *Dentiscutata colliculosa*, a new species in the *Glomeromycetes* from Northeastern Brazil with colliculate spore ornamentation. Nova Hedwigia 90: 383–393. <https://doi.org/10.1127/0029-5035/2010/0090-0383>
- Goto BT, Silva GA, Assis ADM, Silva DKA, Souza RG, Ferreira ACA, Jobin K, Mello CMA, Vieira HEE, Maia LC, Oehl F. 2012. *Intraornatosporaceae* (Gigasporales), a new family with two new genera and two new species. Mycotaxon 119: 117–132. <https://doi.org/10.5248/119.117>
- Goto BT, Araújo AF, Soares ACF, Ferreira ACA, Maia LC, Sousa CS, Silva GA. 2013. *Septoglomus titan*, a new fungus in the *Glomeraceae* (*Glomeromycetes*) from Bahia, Brazil. Mycotaxon 124: 101–109. <https://doi.org/10.5248/124.101>
- INEGI (Instituto Nacional de Estadística y Geografía). 2010. Compendios de información geográfica municipal de los Estados Unidos Mexicanos: Oaxaca. Consulted October 2017: <http://www.inegi.org.mx/geo/contenidos/topografia/compendio.aspx>
- INVAM (International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi). 2018. Species descriptions from reference cultures. West Virginia University. Consulted November 2018: <https://invam.wvu.edu/>
- Khade SW. 2010. *Dentiscutata nigerita*, a new species of arbuscular mycorrhizal fungi from India. Mycosphere 1(3): 241–247.
- Koske ER, Walker C. 1985. Species of *Gigaspora* (*Endogonaceae*) with roughened outer walls. Mycologia 77: 702–720. <https://doi.org/10.1080/00275514.1985.12025159>
- Lekberg Y, Koide TR, Rohr RJ, Aldrich-Wolfe L, Morton BJ. 2007. Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. Journal of Ecology 95: 95–105. <https://doi.org/10.1111/j.1365-2745.2006.01193.x>
- Lin TC, Yen CH. 2011. *Racocetra undulata*, a new species in the *Glomeromycetes* from Taiwan. Mycotaxon 116: 401–406. <https://doi.org/10.5248/116.401>
- Montoya-Martínez AC, Rincón-Enríquez G, Lobit P, López-Pérez L, Quiñones-Aguilar EE. 2019. Native arbuscular mycorrhizal fungi from the rhizosphere of *Agave cupreata* and their effect on *Agave tequilana* growth. Revista Fitotecnia Mexicana 42(4): 429–438. <https://doi.org/10.35196/rfm.2019.4.429-438>
- Morrone JJ. 2019. Regionalización biogeográfica y evolución biótica de México: encrucijada de la biodiversidad del Nuevo Mundo. Revista Mexicana de Biodiversidad 90: e902980. <https://doi.org/10.22201/ib.20078706e.2019.90.2980>
- Oehl F, Souza FA, Sieverding E. 2008. Revision of *Scutellospora* and description of five new genera and three new families in the arbuscular mycorrhiza-forming *Glomeromycetes*. Mycotaxon 106: 311–360.
- Ordoñez MJ, Rodríguez P. 2008. Oaxaca, el estado con mayor diversidad biológica y cultural de México, y sus productores rurales. Ciencias 91: 54–64.

- Polo-Marcial MH, Lara-Pérez LA, Goto BT, Margarito-Vista X, Andrade-Torres A. 2021. *Glomeromycota* in Mexico, a country with very high richness. *Sydowia* 74: 33–63. <https://doi.org/10.12905/0380.sydowia74-2021-0033>
- Reyes-Jaramillo I, Chimal-Sánchez E, Salmerón-Castro JY, Vázquez-Pérez N, Varela-Fregoso L. 2019. Comunidad de hongos micorrizógenos arbusculares (*Glomeromycota*) asociada con agaves mezcaleros de Oaxaca y su relación con algunas propiedades edáficas. *Revista Mexicana de Biodiversidad* 90: e902777. <https://doi.org/10.22201/ib.20078706e.2019.90.2777>
- Silva GA, Maia LC, Oehl F. 2012. Phylogenetic systematics of the *Gigasporales*. *Mycotaxon* 122: 207–220. <https://doi.org/10.5248/122.207>
- Smith ES, Read JD. 2008. Mycorrhizal symbiosis. 3rd Edition. Elsevier Science Publishing Co Inc. United States.
- Souza AF, Silva RI, Barros Barreto MBB, Oehl F, Goto BT, Maia LC. 2018. *Racocetra crispa* (*Glomeromycotina*) delimited by integrative evidence based on morphology, long continuous nuclear rDNA sequencing and phylogeny. *Mycological Progress* 17: 999–1011. <https://doi.org/10.1007/s11557-018-1410-9>
- Stutz JC, Morton BJ. 1996. Successive pot cultures reveal high species richness of arbuscular endomycorrhizal fungi in arid ecosystems. *Canadian Journal of Botany* 74: 1883–1889. <https://doi.org/10.1139/b96-225>
- Tchabi A, Hountondji F, Laouin L, Coyne D, Oehl F. 2009. *Racocetra beninensis* from sub-Saharan savannas: a new species in the *Glomeromycetes* with ornamented spores. *Mycotaxon* 110: 199–209. <https://doi.org/10.5248/110.199>
- Torres-García I, Rendón-Sandoval FJ, Blancas J, Casas A, Moreno-Calles AI. 2019. The genus *Agave* in agroforestry systems of Mexico. *Botanical Sciences* 97(3): 263–290. <https://doi.org/10.17129/botsci.2202>
- Varela L, Hernández-Cuevas LV, Chimal-Sánchez E, Montaña NM. 2019. Taxonomic diversity of arbuscular mycorrhizal fungi cited from Mexico. In: J Álvarez-Sánchez & al. (eds). *Biodiversidad de Microorganismos de México: Importancia, Aplicación y Conservación*. 1a. ed. electrónica, UNAM, México. 1487 p.
- Vieira LC, Silva DKA, Escobar IEC, Silva JM, Moura IA, Oehl F, Silva GA. 2020. Changes in an arbuscular mycorrhizal fungi community along an environmental gradient. *Plants* 9(52):[16p.]. <https://doi.org/10.3390/plants9010052>
- Walker C. 1983. Taxonomic concepts in the *Endogonaceae*: spore wall characteristics in species descriptions. *Mycotaxon* 18: 443–455.
- Wijayawardene NN, Hyde DK, Al-Ani LKT, Tedersoo L, Haelewaters D, Rajeshkumar KC & al. 2020. Outline of fungi and fungi-like taxa. *Mycosphere* 11(1): 1060–1456. <https://doi.org/10.5943/mycosphere/11/1/8>
- WRB. 2014. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome. 186 p.